CONTRIBUTIONS TO PALÆONTOLOGY

I

PLESIPPUS FRANCESCANA (FRICK) FROM THE LATE PLIOCENE, COSO MOUNTAINS, CALIFORNIA

With a

REVIEW OF THE GENUS PLESIPPUS

By John R. Schultz

With three plates and three text-figures

[Preprinted from Carnegie Institution of Washington Publication No. 473, pages 1 to 13, May 21, 1936]

CONTRIBUTIONS TO PALÆONTOLOGY

I

PLESIPPUS FRANCESCANA (FRICK) FROM THE LATE PLIOCENE, COSO MOUNTAINS, CALIFORNIA

With a

REVIEW OF THE GENUS PLESIPPUS

By John R. Schultz

[Issued May 21, 1936]

CONTENTS

PLESIPPUS FRANCESCANA (FRICK) FROM THE LATE PLIOCENE, COSO MOUNTAINS, CALIFORNIA

INTRODUCTION

Two mammalian types, occurring in a late Pliocene fauna from the Coso Mountains, California, have already been described.[1] Among the more abundant forms in this assemblage are the horses of the genus *Plesippus*. These are of particular interest not only for purposes of correlation of the geologic horizon in which they occur, but also because of their phylogenetic relationships. Opportunity is taken therefore to make a comparative study of characters of the species from the Coso Mountains with reference to nearly related forms found in beds of similar age and to define more clearly, than has been previously attempted, the position of *Plesippus* in the lineage of the horse group.

The writer is under obligation to Dr. Chester Stock for opportunity to study the collection, for critical reading of the manuscript, and for his constant interest and guidance during the investigation. Messrs. E. L. Furlong and R. W. Wilson have contributed valuable discussions and suggestions. Thanks are expressed to the Los Angeles Museum for permission to study the mounted specimen of *Plesippus shoshonensis*, and to the U. S. National Museum for loan of material representing this species from Hagerman, Idaho. The type of *Plesippus francescana* was loaned through the kindness of the Museum of Palæontology, University of California. The illustrations have been prepared by Mr. John L. Ridgway.

LIST OF LOCALITIES

Calif. Inst. Locality 118—Immediately north of the Snake River, thirteen miles northwest of Grand View, Ada County, Idaho. (*Plesippus idahoensis.*)

Calif. Inst. Locality 119—On south side of the Snake River and opposite locality 118, Owyhee County, Idaho. (*Plesippus idahoensis.*)

Calif. Inst. Locality 131—Western flanks of Coso Mountains east of Olancha, Inyo County, California. The Coso Range forms a southward topographical continuation of the Inyo Mountains and bounds the southeastern portion of Owens Valley. (*Plesippus francescana.*)

Calif. Inst. Locality 210—U. S. National Museum quarry site on the Snake River near Hagerman, Idaho. (Type of *Plesippus shoshonensis.*)

Calif. Inst. Locality (unnumbered)—Valley of Tres Pinos Creek near its junction with Los Muertos Creek, San Benito Quadrangle, California. (*Plesippus proversus.*)

Univ. of Calif. Locality 2079—North Coalinga region, western border of the San Joaquin Valley, California, Upper Etchegoin formation. (Type of *Plesippus proversus.*)

[1] R. W. Wilson, Jour. Mammalogy, vol. 13, 150–154, 1932; C. Stock, *ibid.*, vol. 13, 263–266, 1932.

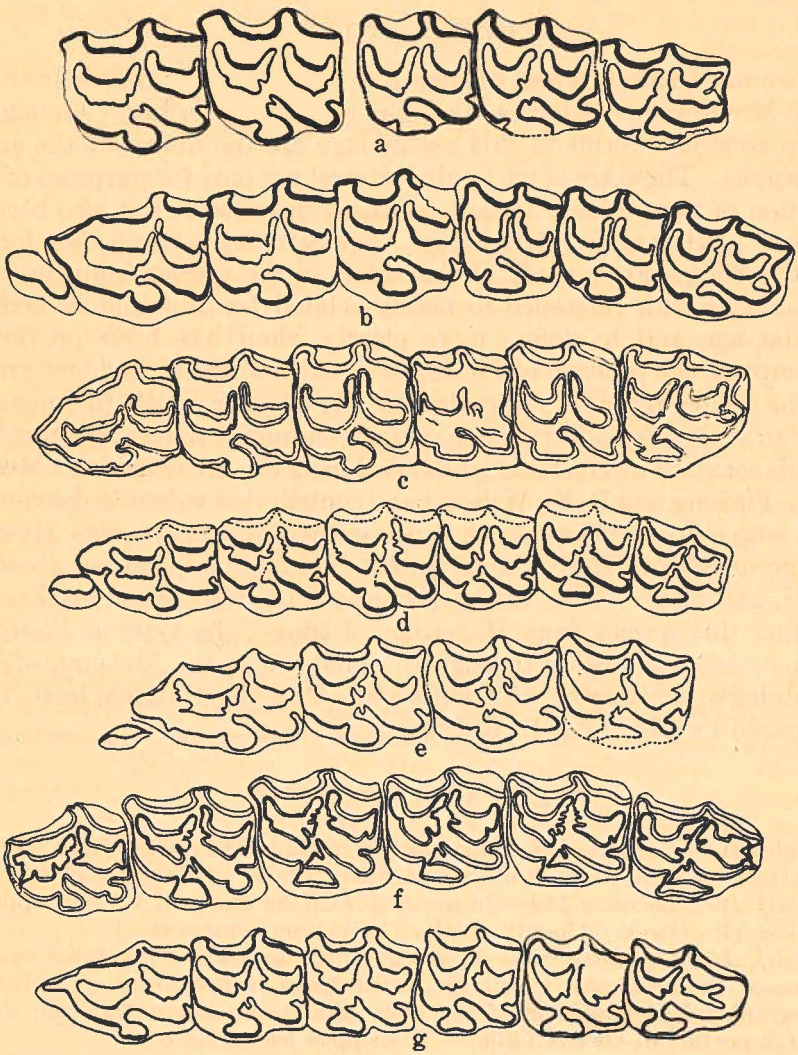


FIG. 1—Upper cheek-tooth series of species of *Plesippus*. a, type of *P. francescana* (Frick), No. 23277 Univ. of Calif. Coll., Loc. 3253, right side (reversed in printing); b, *P. francescana*, referred specimen, No. 847, Calif. Inst. Loc. 131, right side reversed (in printing); c, *P. simplicidens* (Cope) after Matthew (reversed); d, *P. proversus* (Merriam); e, *P. shoshonensis* Gidley; f, *P. idahoensis* (Merriam), No. 1852, Calif. Inst. Loc. 119; g, *P. idahoensis* (Merriam), No. 892, Calif. Inst. Loc. 118. All figures $\times \frac{1}{2}$.

Univ. of Calif. Locality 3036C—Near Froman Ferry on the Snake River, eight miles southwest of Caldwell, Idaho, Idaho formation. (Type of *Plesippus idahoensis*.)

Univ. of Calif. Locality 3253—Elsinore Quadrangle, central portion of SE ¼ Sec. 9, T. 3S, R. 2W., Upper San Timoteo beds. (Type of *Plesippus francescana*.)

Univ. of Texas—Crosby County, Texas, Blanco Canyon bed. (Type of *Plesippus simplicidens*.)

Univ. of Texas—Mont Blanco, Crosby County, Texas, Blanco formation. (Type of *Plesippus cumminsii*.)

Plesippus francescana (Frick)

Although no complete skulls were found, the collection from the late Pliocene beds of the Coso Mountains includes several series of upper and lower teeth, jaws, and numerous skeletal elements. Comparison with specimens of *Pliohippus francescana* Frick from the San Timoteo beds of southern California fails to disclose any difference except that of size. Consequently the material from the Coso Mountains is referred to Frick's species. The collection now available permits a supplementary description of this form. Additional characters are: (1) presence of a large and functional P1, (2) nearly vertical position of the upper incisors, (3) flattening of the protocone in the last two premolars, (4) presence of a vestigial protostylid in individual lower cheek-teeth, (5) characters of the milk dentition. Reasons for referring the species to *Plesippus* rather than to *Pliohippus* will be more fully discussed elsewhere in this paper.

DESCRIPTION OF MATERIAL

Material—A mandible, No. 902 (Plate 1); a series of upper cheek-teeth, No. 847 (Plate 2, fig. 2); three upper milk teeth, No. 1847 (Plate 2, figs. 3 and 4); three lower milk teeth, No. 1848 (Plate 2, fig. 1); numerous fragmentary mandibular rami and maxillaries; various limb elements. All specimens in the collection of the California Institute of Technology and from Calif. Inst. Tech. Vert. Pale. Locality 131.

General Characters of Skull and Dentition—The mandibular specimens indicate a form of large size, comparable in this character to *Equus caballus*. The cheek-teeth are long with moderately curved and well-cemented crowns. The incisors have a procumbent position approximately like that in the modern genus. A large and functional P1 is always present. Since a detailed description of the permanent cheek-teeth would merely result in a repetition of Frick's exposition,[1] it has been omitted.

Upper Deciduous Cheek-Teeth—In these teeth the parastyles are larger and flatter than the mesostyles. The external borders of the fossettes are round. Both fossettes are moderately broad, and their borders show few plications. A well-developed posthypoconal valley lends an oval shape to the hypocone in Dp2 and Dp3, and an irregular, pointed outline to this cusp in Dp4. The protocone approximates an oval in shape in Dp2, but is flattened and is slightly indented in the remaining milk-teeth. A single pli caballin is present. For illustrations see Plate 2, figures 3 and 4.

Lower Deciduous Cheek-Teeth—A striking feature is the presence of an anteroexternal enamel fold (protostylid) on the protoconid. A similar fold

[1] Childs Frick, Univ. Calif. Pub., Bull. Dept. Geol., vol. 12, 322-333, 1921.

is present in lower milk teeth of *Plesippus shoshonensis*. It is probable that a protostylid will be found in deciduous teeth of allied species of *Plesippus*, since it occurs in milk-teeth of *Equus occidentalis*. A vestige of this fold is present in permanent teeth of some species of *Pliohippus* [1] and in *Plesippus simplicidens* [2] and *P. francescana*.

The external walls of the protoconid and hypoconid are convex. A single subsidiary fold marks the posterior, internal border of the median external valley. The valley extends approximately one-third of the distance from the outer side of the internal groove in Dp2, very nearly to the gutter in Dp3, and touches the enamel of this groove in Dp4. The gutter is sharply V-shaped in Dp2, but is broader and less deeply incised in the remaining teeth. The metastylid is nearly oval in shape in Dp2, and approaches the

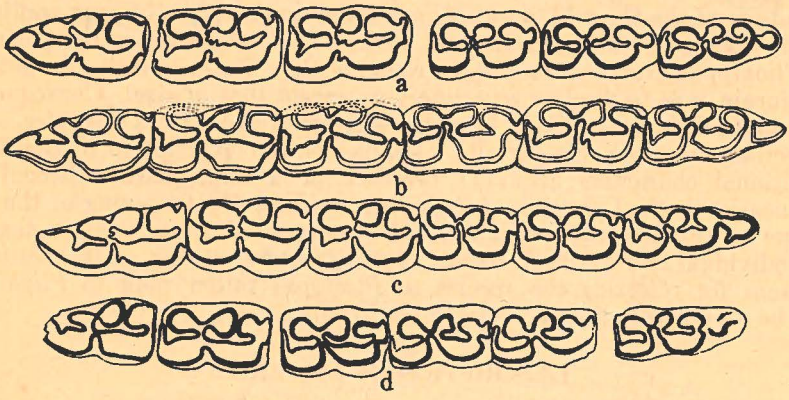


FIG. 2—Lower cheek-tooth series of *Plesippus*. a, *P. francescana* (Frick), No. 902, Calif. Inst. Loc. 131; b, *P. simplicidens* (Cope), after Cope; c, *P. shoshonensis* Gidley, No. 1581, Calif. Inst. Loc. 210; d, *P. idahoensis* (Merriam), No. 892, Calif. Inst. Loc. 118. All figures ×½.

metaconid in size, but is smaller than this cusp in the posterior teeth. A markedly rounded outline characterizes the entoconid. The hypoconulid is expanded transversely both internally and externally in Dp4, very slightly internally and very greatly externally in Dp3, and only internally in Dp2. These teeth are illustrated in Plate 2, figure 1.

Limb and Foot Elements—The distal ends of the tibia and fibula are fused as completely as in the modern species. Carpals and tarsals are more slender than the corresponding elements in *E. caballus*. The metapodials are relatively slender, but approach in their proportions those of the living form. None of the lateral digits is complete at the distal end, but it is probable that these elements did not extend more than three-quarters of the length of the cannon bone. The ungual phalanges are small (see Plate 3).

Measurements—The following measurements are taken according to the system employed by Merriam.[3] Specimen No. 1846 is worn slightly more than No. 847.

[1] H. F. Osborn, Mem. Amer. Mus., n. s., vol. 2, pt. 1, 146, 1918.
[2] J. W. Gidley, Bull. Amer. Mus., vol. 14, 125, 1901.
[3] J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 7, 409, 1913.

Measurements (in millimeters)

PERMANENT DENTITION

	No. 847	No. 1846
Length of upper molar-premolar series with P1	201	.....
Length of upper premolar series without P1	104	.....
Length of upper molar series	84	83.5
P2 anteroposterior diameter	40.8	.....
P2 transverse diameter	30.4	.....
P3 anteroposterior diameter	32.8	31
P3 transverse diameter	32	35.4
P4 anteroposterior diameter	31.3	30
P4 transverse diameter	31	33.5
M1 anteroposterior diameter	25	23.4
M1 transverse diameter	27.2	31.2
M2 anteroposterior diameter	26	28.5
M2 transverse diameter	28	30
M3 anteroposterior diameter	32.3	31.6
M3 transverse diameter	25.6	27.5

	No. 849	No. 902
Length of lower molar series	89	91
Length of lower premolar series	.....	102
P2 anteroposterior diameter	.....	36.8
P2 transverse diameter	.....	16.5
P3 anteroposterior diameter	32.2	32.8
P3 transverse diameter	16	17
P4 anteroposterior diameter	31.8	32.8
P4 transverse diameter	15.3	16.8
M1 anteroposterior diameter	28.7	27.8
M1 transverse diameter	13.8	14.8
M2 anteroposterior diameter	29	29.8
M2 transverse diameter	13.2	13.8
M3 anteroposterior diameter	31	31.4
M3 transverse diameter	10	12.8
I1 greatest transverse diameter	.....	9.5
I2 greatest transverse diameter	.....	9.5
C greatest anteroposterior diameter	.....	14

MILK DENTITION

	No. 1847
Dp2 anteroposterior diameter	.....
Dp2 transverse diameter	22.4
Dp3 anteroposterior diameter	33
Dp3 transverse diameter	21.6
Dp4 anteroposterior diameter	34
Dp4 transverse diameter	22.6
Dp4 length of crown	41
	No. 1848
Dp2 anteroposterior diameter	38
Dp2 transverse diameter	13.4
Dp3 anteroposterior diameter	33
Dp3 transverse diameter	13.3
Dp4 anteroposterior diameter	34
Dp4 transverse diameter	13.2

ADDITIONAL SPECIES REFERRED TO PLESIPPUS

Plesippus simplicidens (Cope) [1]—Figures 1c and 2b illustrate the characters of the upper and lower cheek-tooth series of this species. The type was originally assigned to *Equus*, but was referred to *Pliohippus* by Gidley.[2] Matthew[3] on the basis of material referred to this species, established the genus *Plesippus*.

[1] E. D. Cope, Proc. Amer. Philos. Soc., vol. 30, 124–125, 1892.
[2] J. W. Gidley, Bull. Amer. Mus., vol. 14, 125, 1901.
[3] W. D. Matthew, Amer. Mus. Novitates, No. 131, 1924.

Plesippus cumminsii (Cope) [1]—This species is based on very fragmentary material. It appears to be closely related to *P. simplicidens,* and, following Matthew and Stirton,[2] may readily be referred to the same genus. Both forms were described from the Blanco beds of Texas.

Plesippus proversus (Merriam) [3]—This species, based on several upper and lower teeth, was described by Merriam from the Upper Etchegoin horizon of California. Merriam assigned the species to *Pliohippus,* but appreciated the advanced characters of the type as implied by the specific name. The form was later referred to *Plesippus* by Matthew.[4] Since this description the same species has been recognized by Russell and Vander Hoof [5] in a late Pliocene mammalian fauna from northern California. The tooth-row illustrated in figure 1d belongs to a skull of *Plesippus proversus* embedded in a boulder found in a stream bed several miles south of Hollister, San Benito County, California. Unfortunately the source of the boulder is not determined.

Additional tooth-characters furnished by this new material are: (1) a rather marked anterior projection of the protocone in all teeth except P2, (2) the flattened or indented inner wall of the protocone in the cheek-teeth, except in the second and fourth upper premolars, (3) moderate width of the isthmus except in P4 where it is noticeably wider, and (4) presence of a functional P1.

Plesippus shoshonensis Gidley [6]—Figure 1e shows the pattern of the upper dentition of No. 1863 from the Hagerman locality in Idaho, while figure 2c illustrates the lower tooth-row of specimen No. 1581, Calif. Inst. Tech. Vert. Pale. Coll. from the same locality. Moderately worn upper molars exhibit greatly elongated protocones, the inner margins of which are flattened but not indented. The anterior projection of this cusp beyond the level of the isthmus is marked. The isthmus is usually quite narrow.

In the lower cheek-tooth series, the proto- and hypoconids are moderately flattened in the premolars; in the molar series, however, these pillars are markedly rounded. The internal groove or gutter is sharply V-shaped at its outermost extremity, but is seen to broaden out rapidly toward the median plane of the jaw.

A palate and dentition of a young individual of *P. shoshonensis,* No. 1783, shows the protocone to be somewhat flattened and indented in the milk-teeth. An interesting feature of this specimen is the union of the post-protoconal valley and prefossette. Individual lower milk-teeth possess a well-developed protostylid; one specimen, No. 1851 (fig. 3b), shows the presence of a posterior, external fold (hypostylid).

Plesippus idahoensis (Merriam) [7]—*Equus idahoensis* was described on the basis of two teeth found near Froman Ferry on the Snake River, Idaho. Specimen No. 892 (figs. 1g, 2d) representing a fragmentary skull with dentition, found near Grand View, Idaho, C.I.T. Locality 118, is referred to this species. The skull proportions are similar to those in *E. caballus.* P1 is represented by a vestige on the right side of the palate. The protocone

[1] E. D. Cope, 4th Ann. Rept. Geol. Surv. Texas, 67, 1893.

[2] W. D. Matthew and R. A. Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 19, 359, 1930.

[3] J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 9, 525–534, 1916.

[4] W. D. Matthew, *op. cit.* 2, 1924.

[5] R D. Russell and V. L. Vander Hoof, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 20, 17–19, 1931.

[6] J. W. Gidley, Jour. Mammalogy, vol. 11, 300–301, 1930.

[7] J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 10, 527–530, 1918.

KEY TO SPECIES OF PLESIPPUS

	FRANCESCANA	SIMPLICIDENS	PROVERSUS	SHOSHONENSIS	IDAHOENSIS
PROTOCONE	Usually flat, very slight indentation and projection. Length moderate.	Flat. Very little indentation. Projects only in molars. Length moderate.	Flat and moderately indented. Projection moderate. Length moderate.	Flat. Seldom indented. Projection marked. Length great.	Flat. May or may not be indented, but usually markedly so. Projection moderate to great. Length moderate to great.
CURVATURE	Marked to moderate.	Moderate.	Moderate.	Very moderate.	Nearly straight.
FOSSETTES	Moderately broad. Plications few.	Moderately broad. Plications few.	Large moderately complicated borders.	Moderately broad. Borders moderately complicated.	Large, complicated.
PROTO- AND HYPOCONID	Convex. Protostylid vestigial.	Slightly flat. More nearly round in molars. Protostylid vestigial.	Convex to slightly flat.	Convex to flat Hypoconid usually the flatter.	Nearly flat in the premolars. More nearly round in the molars.
GUTTER	Sharp V in premolars. Apex flat in molars.	Wide but pointed at apex.	Round V to open.	V-shaped.	V-shaped to broadly open in premolars.

shows a marked anterior projection in all teeth except in P2. The very slight indentation of the inner wall of this cusp is largely the result of an advanced stage of wear.

The protoconid and hypoconid have rounded faces in the molars, but these are noticeably flattened in the premolars. The metaconid-metastylid groove opens more widely in the premolars than in the molars. In the latter it forms a V-shaped incision.

A single specimen, No. 1852 (fig. 1f), from C. I. T. locality 119 near Grand View, Idaho, is doubtfully referred to this species. The major differences between this specimen and No. 892 are: (1) narrower isthmus, and (2) less-marked indentation of inner wall of protocone and shorter anterior projection of this cusp. These differences appear to be due principally to individual variation, since both specimens show approximately the same stage of wear. These two individuals appear to be closely related and may be specifically identical. Reasons for referring the species to *Plesippus* rather than to *Equus* are given at the end of the following section.

STATUS OF THE GENUS PLESIPPUS

If controversial species, here assigned to *Plesippus*, are excluded from *Pliohippus*, the latter genus is characterized by the following tooth characters: [1] (1) cheek-teeth strongly incurved, (2) isthmus broad in upper cheek-teeth, (3) protocone round-oval in shape, (4) pre- and postfossettes broad, enamel borders with few or no plications, (5) outer walls of protoconid and hypoconid rounded, (6) metaconid-metastylid gutter sharply V-shaped.

Excluding from *Equus* those species that are referred to *Plesippus*, we note that the former genus possesses the following characters: (1) cheek-teeth with nearly straight crowns, (2) isthmus narrow, (3) protocone elongated, indented, and with marked anterior projection, (4) borders of pre- and postfossettes usually with numerous plications, (5) proto- and hypoconids with flattened or slightly concave external walls, (6) metaconid-metastylid groove broadly open.

The striking feature of the forms assigned to *Plesippus* is that they partake individually of both *Pliohippus* and *Equus* characters. Among these species some show considerable resemblance to *Pliohippus*, while others approximate in their characters the genus *Equus*. The intermediate types of the series can be assigned with equal right to either genus. Recognizing *Plesippus* as a subgenus of *Equus*, as Stirton [2] has done, has the disadvantage of vitiating the unity of characters which defines the latter genus, while an assignment to *Pliohippus* likewise destroys the unity of characters of that genus. Determination of border-line species in the classification would still remain a difficult task. However, this difficulty can not be entirely removed by any classification. If, on the other hand, the intermediate position of *Plesippus* is recognized, proper generic reference of end members becomes a matter of considerably less importance. Total elimination of the genus would merely serve to raise the objections stated above, but to a still more marked degree.

Intergradation of specific and generic characters has been discussed recently by Bode,[3] who has shown that recognition of this fact is a natural

[1] Slightly modified after H. F. Osborn, *op. cit.* 146, 1918.
[2] R. A. Stirton, Cordilleran Sec. G. S. A., 33d Ann. Meeting, 37, 1934.
[3] F. D. Bode, Carnegie Inst. Wash. Pub. No. 453, 61–63, 1934.

outcome of increased knowledge of fossil faunas. It is to be expected that certain genera are intermediate in their structural features, but this fact alone does not imply necessarily that a particular genus is invalid, for if the complete fossil record of a family were known all genera would presumably grade into each other. Where genera are to be recognized at all, they must be defined so as to emphasize relationships. In view of these considerations it appears advisable to retain *Plesippus* in full generic rank, and to assign to the genus all species possessing characters of both *Pliohippus* and *Equus*.

P. francescana has been transferred from *Pliohippus* to *Plesippus* for the following reasons. In the upper teeth the characters of the fossettes are typically *Pliohippus*-like. The protocones, however, show some of the characters of *Equus*, for example, their great length, slight anterior projection beyond the isthmus, and slight indentation of their inner faces. The lower teeth resemble those of *Pliohippus* in all details except the flattening of the hypoconid in the premolars.

Equus idahoensis, on the other hand, has been assigned to *Plesippus* principally because, notwithstanding the characters of the upper teeth which resemble those of *Equus*, the lower dentition retains many *Pliohippus* characters. Among these are: the V-shaped metaconid-metastylid groove and the more or less convex faces of the proto- and hypoconids.

ANCESTRY OF THE EQUUS

The illustrations of the series of cheek-teeth of the several species of *Plesippus* (figs. 1 and 2) show a striking gradation of characters from *Pliohippus* to *Equus*. Moreover, the occurrence of *Plesippus* in the late Pliocene and possibly early Pleistocene is in accord with the intermediate position which this form holds between the latter genera. It seems apparent that the gradation in characters indicates a relationship between the Pliocene *Pliohippus* and Pleistocene *Equus*. Retention of an intermediate genus, namely *Plesippus*, therefore marks that genus as an ancestor of *Equus*.

The characters in the dentition of *Pliohippus* are quite constant as are likewise those in various species of *Equus*. Examination of a large series of specimens of *E. occidentalis* from the McKittrick Pleistocene of California reveals the fact that while minor variations occur, much less individual difference exists among these forms than among either *Plesippus francescana* or *P. idahoensis*. An inference may be drawn that the tooth-characters of *Plesippus* were in a mobile or unstable state, possibly the result of rather rapid evolution of the group.

Whether this development in time was directional and marked by gradual and progressive modification of essential dental characters, or whether it was a more or less random process, can not be definitely determined at present. With regard to the material at hand, it is important to recognize that in all cases the lower premolars are more advanced than the molars. This is not only true for the specimens figured, but has been observed in all the material studied. The illustrations, figures 1 and 2, are arranged in an attempt to show the probable phylogenetic sequence. Not all of the evidence supports this arrangement. Thus, as mentioned on a preceding page, the pre-fossette is united with the post-protoconal valley in milk-teeth of *P. shoshonensis*, while the two are separate in deciduous teeth of *P. francescana*. On this character alone *P. shoshonensis* would appear to be a more primitive type than *P. francescana*. On the other hand, the

structural features of the permanent dentition seemingly indicate that *P. shoshonensis* is more advanced. This conflicting evidence tends to cast doubt on the assumption that evolution was progressive in all characters, and practically eliminates the possibility of constructing a satisfactory phylogenetic chart.

With reference to possible correlation of the instability of characters seen in the *Plesippus* group with rapidly changing environmental conditions, it should be mentioned that the late Pliocene marks a time of critical conditions immediately antecedent to the coming of the Ice Age.

PLESIPPUS-LIKE TYPES OF EURASIA AND NORTHERN AFRICA

Boule [1] has shown that the European *Equus stenonis* of the late Pliocene and early Pleistocene comprises two quite diverse types. According to this author the first or *Equus caballus* type is characterized by long, indented protocones, complicated fossette borders, and large and fluted styles in the upper dentition; the second or *E. stenonis* type is characterized by teeth possessing shorter protocones, which are not indented and which do not project so far anteriorly. This form is further distinguished by simple fossette borders, and smaller, non-bifurcate styles. In the lower dentition

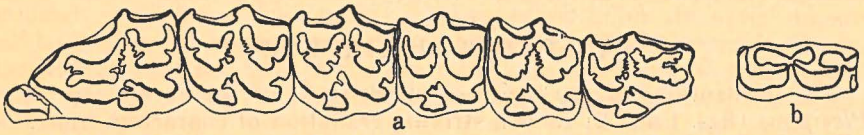


FIG 3—a, *Equus? stenonis* Cocchi, after Forsyth Major; b, *P. shoshonensis* Gidley, lower milk tooth, No. 1851, Calif. Inst. Loc. 210. ×½.

the protoconid and hypoconid are rounded as are also the metaconid and metastylid, and the latter are separated by a V-shaped notch. Figure 3a illustrates the characters of this group.

It is apparent that the dental characters of the *E. stenonis* type correspond almost exactly with those of *Plesippus*, as defined on pages 10–11 of this paper. On the other hand, those of the *E. caballus* type are more like the characters seen in North American horses of the later Pleistocene. The bifurcation of the styles does not appear to be a constant character among North American species of *Equus*. It would appear, therefore, that this feature possesses little diagnostic value. However, the styles are never bifurcate in *Plesippus*.

Another character pointed out by Boule is the presence of a postero-external cuspule (hypostylid) in lower milk-teeth of *E. stenonis* and of closely related forms, *E. asinus atlanticus* and *E. burchelli*. This cuspule is absent in deciduous teeth of *E. asinus* and *E. caballus*. Boule [2] concluded that *E. stenonis* gave rise to *E. caballus* (not to be confused with the *E. caballus* type or subspecies of *E. stenonis*), while a persistently primitive branch of the same species, *i.e. E. stenonis*, is represented by the modern zebra. He also concluded that the Pleistocene forms of Europe are all of the *E. caballus* type, and that the ancestor of the European *E. stenonis* is to be found in *Protohippus* of North America.[3]

[1] Marcellin Boule, Bull. Soc. Géol. de France, Ser. 3, vol. 27, 531–542, 1899.
[2] M. Boule, *op. cit.* 532, 534, 542, 1899.
[3] M. Boule, Annales de Paléontologie, Tome 5, 18, 1910.

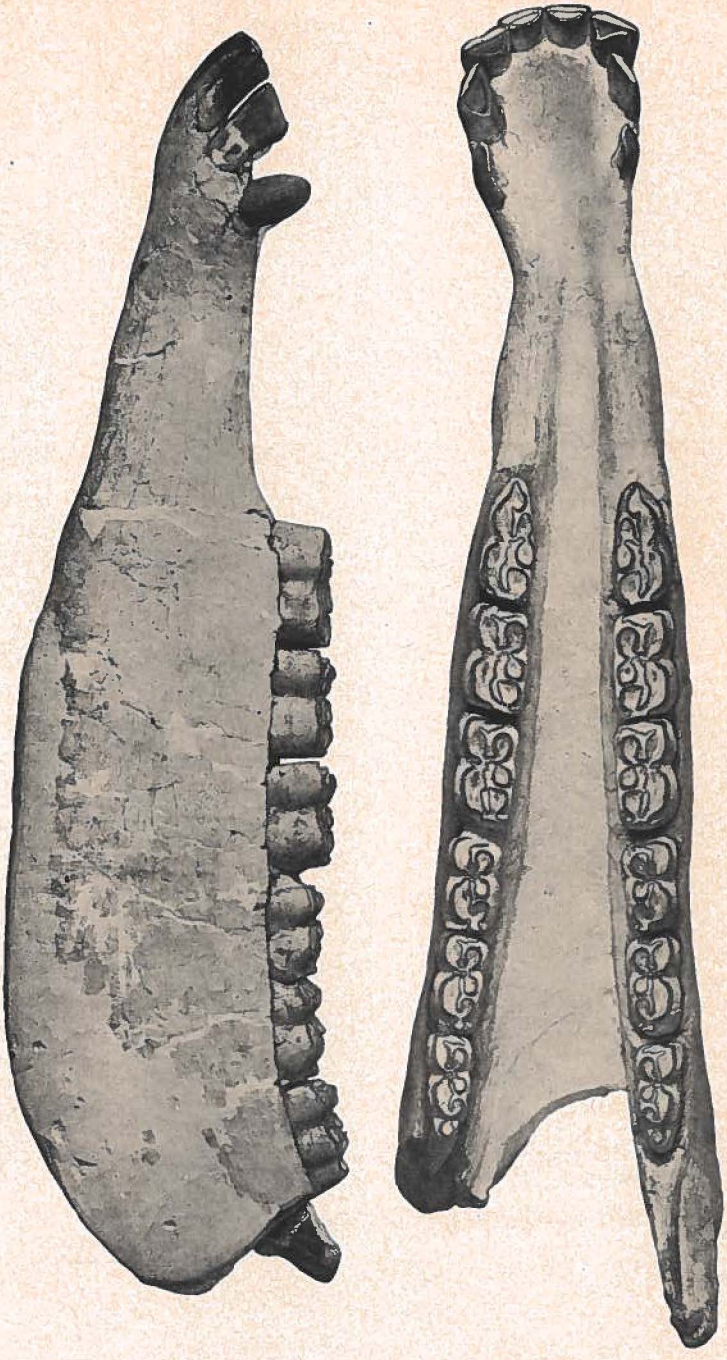
Figure 3b illustrates a lower milk molar, No. 1851 from C. I. T. Locality 210, of *Plesippus shoshonensis*. The feature of particular interest about this tooth is the presence of a hypostylid similar to that described by Boule in milk-teeth of *E. stenonis* and of related forms. This evidence in addition to that already discussed, suggests that the *E. stenonis* type, as defined by Boule from the late Pliocene of Europe, falls within the *Plesippus* group of North America, and is perhaps a descendant of some species of the latter genus. In other words, the differences between the two European types grouped under a single species, namely *E. stenonis*, are here considered to be of generic value. Boule's *E. stenonis* type from the late Pliocene of Europe becomes *Plesippus stenonis*, while his *E. caballus* type from the European early Pleistocene is retained in *Equus*, and may be designated *Equus stenonis*.

In this connection it should be noted that *E. sivalensis* of the Siwalik beds of India was regarded by Forsyth Major [1] as identical with *E. stenonis*. Judging from Lydekker's remarks,[2] one may conclude that *E. sivalensis* is allied with the true *Equus* rather than with the *Plesippus* group. *E. stenonis* is found also in the late Pliocene Norwich Crag of England.[3] These deposits contain *Mimomys*, a genus of vole closely related to *Cosomys* of the Coso Mountains. No illustrations of *E. stenonis* from the Norwich Crag are available, but it is inferred that this species belongs to the *Plesippus* group. Recognition of the primitive forms of *E. stenonis* as *Plesippus* may facilitate late Tertiary and early Pleistocene correlation between Eurasia, Northern Africa,[4] and North America, as well as aid in establishing a fairly sharp faunal demarcation between the two periods.

It is interesting to recall that Merriam [5] suggested a possible relation of *Plesippus proversus* from the Upper Etchegoin of California to *Equus stenonis* of the Old World. He considered the time represented by the late Pliocene or early Pleistocene Tulare beds of California as sufficient to permit migration from North America to Europe.

In a recent paper, Colbert [6] regards *Plesippus* as intermediate between *Pliohippus* and *Equus*, and expresses the view that the *Equus* forms of the Upper Siwalik are derived from North American ancestors. Colbert concludes that since the first appearance of *Equus* in North America is at the base of the Pleistocene, the Upper Siwalik is Pleistocene in age.

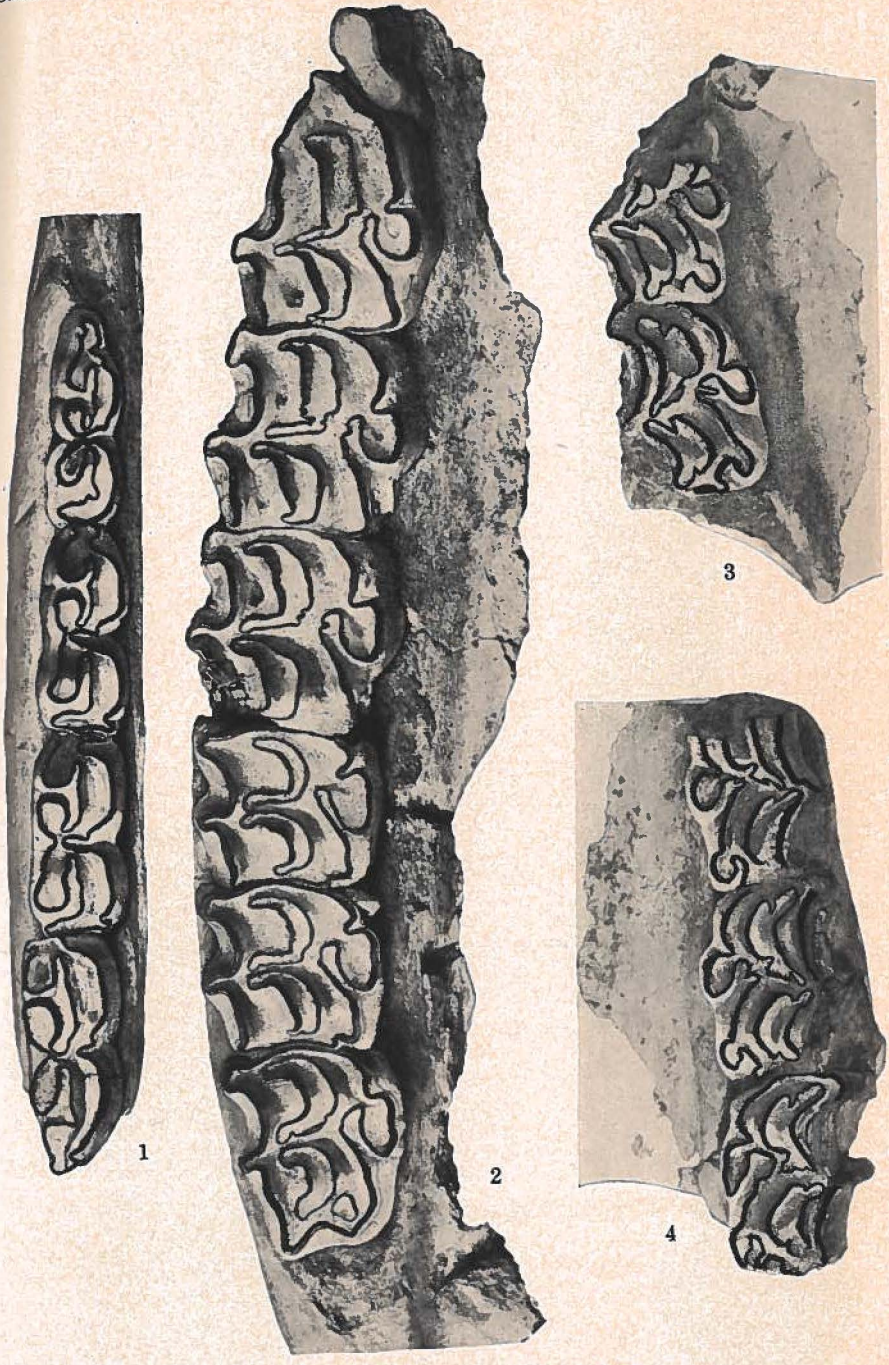
[1] C. J. Forsyth Major, Quart. Jour. Geol. Soc. London, vol. 41, 3, 1885.
[2] R. Lydekker, Palæontologia Indica, Ser. X, vol. 2, plates XIV, XV, 1881–84.
[3] J. W. Evans and C. J. Stubblefield, Handbook of the Geol. of Great Britain, 435, 1929.
[4] R. Lydekker, Quart. Jour. Geol. Soc. London, vol. 43, 161–163, 1887.
[5] J. C. Merriam, *op. cit.* 532–533, 1916.
[6] E. H. Colbert, Amer. Mus. Nat. Hist. Novitates, No. 797, 11–12, 1935.



Plesippus francescana (Frick)

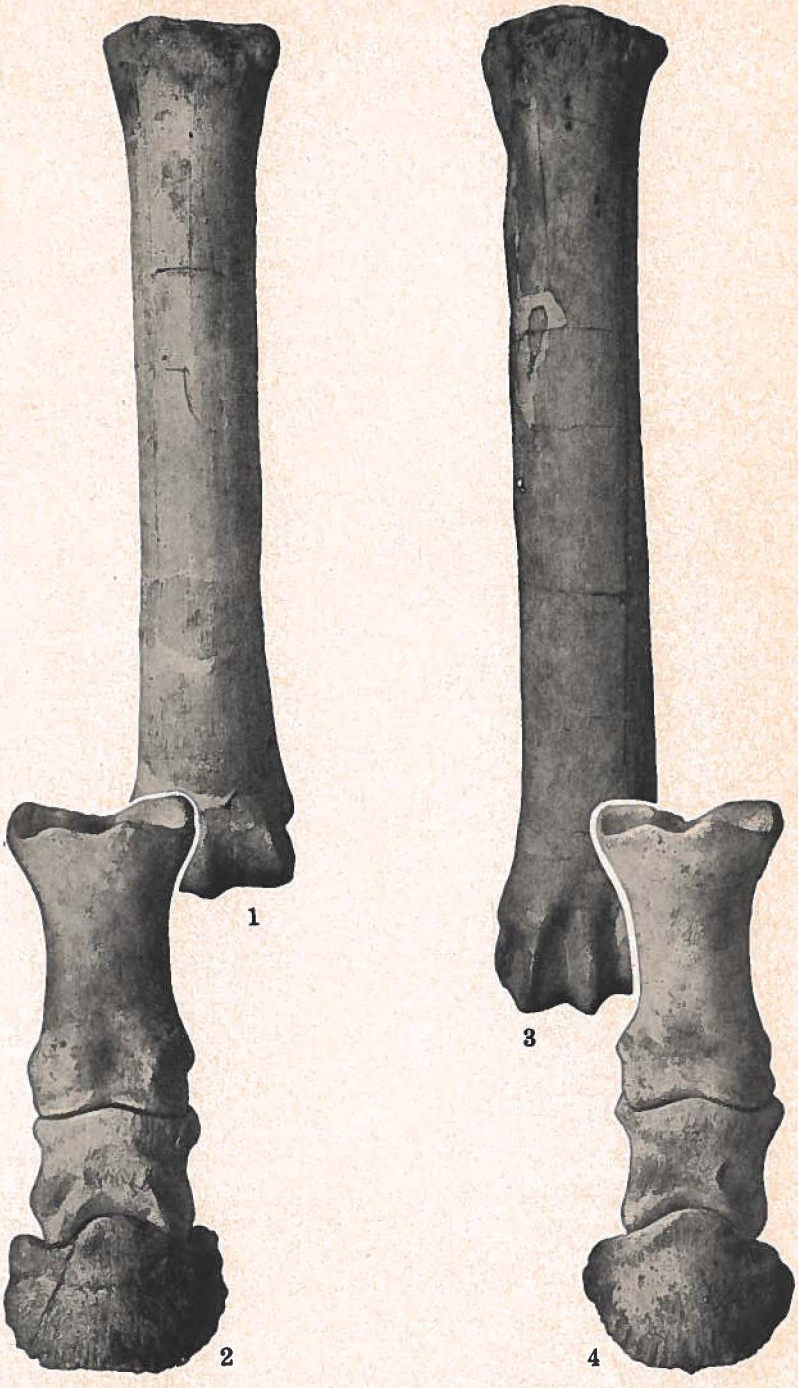
No. 902, mandible, lateral and occlusal views. The symphyseal end has been bent a trifle downward. Approx. 2/5 nat. size.

Calif. Inst. Tech. Vert. Pale. Coll. Pliocene, Coso Mountains, Calif.



Plesippus francescana (Frick)

FIG. 1—Left ramus with Dp$\bar{2}$–$\bar{4}$ and M$\bar{1}$, No. 1848.
FIG. 2—Deeply worn upper cheek-tooth series, No. 847.
FIGS. 3, 4—Dp$\underline{2}$, Dp$\underline{3}$ of right side and Dp$\underline{2}$–$\underline{4}$ of left side, No. 1847.
All figures approx. 4/5 nat. size.
Calif. Inst. Tech. Vert. Pale. Coll. Pliocene, Coso Mountains, Calif.



Plesippus francescana (Frick)

FIG. 1—Right metacarpal III, No. 1924.
FIG. 2—Phalanges, Nos. 1925, 1926, 1927.
FIG. 3—Right metatarsal III, No. 1923.
FIG. 4—Phalanges, Nos. 1928, 1929, 1930.

All figures 1/2 nat. size.
Calif. Inst. Tech. Vert. Pale. Coll. Pliocene, Coso Mountains, Calif.